

Evolution, biogeography, and description of a new species of Fruit-eating bat, genus *Artibeus* Leach (1821), from Panamá

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Receipt of Ms. 15. 3. 1993
Acceptance of Ms. 6. 6. 1994

Abstract

We describe and name a new species of Neotropical fruit-eating bat, genus *Artibeus*. It is a local endemic, found only on Isla Escudo de Veraguas, approximately 18 km off the Caribbean coast of the province of Bocas del Toro in northwestern Panamá. Based on a variety of shared characters we assume that this new species has evolved from a species also ancestral to *Artibeus watsoni*, which is widespread and abundant on the mainland and other islands of Bocas del Toro. The new species is 15% larger in mass than its mainland relative, 10% larger in body dimensions, and 6% larger in cranial dimensions. Several discrete morphological characters, particularly in the dentition, also distinguish this bat from *A. watsoni*. We discuss aspects of evolution and biogeography of *A. incomitatus* to elucidate factors which might have facilitated its speciation.

Introduction

Laguna de Chiriquí on the Caribbean coast of northwestern Panamá (province of Bocas del Toro, 30 km southeast of the Costa Rican boundary) harbors numerous islands (Fig. 1), all formed by rising sea level. The islands are small (the largest is only 59 km²), are close to the mainland, and with one exception they lie in shallow water. Isla Escudo de Veraguas (hereafter, "Escudo"), is the exception. It is surrounded by deeper water and is relatively remote, approximately 18 km off the coast of the mainland and 50 km from the nearest of the other Bocas islands.

Most of the islands, except the smallest, are to some degree inhabited by people. Originally, all of the islands with dry ground were covered with evergreen forest. In recent centuries, repeated disturbance by humans has caused the extirpation of some of the fauna and has removed part or all of the old (primary) forest from most of the islands.

There has been surprisingly little interest in biological exploration of these islands. WETMORE in 1958, HANDLEY in 1960, 1962, and 1963, and DALY and MYERS in 1967 made brief forays to the islands. Recently, a group from the Smithsonian Institution initiated inventories and in-depth studies of the island ecosystems. Its annual expeditions from 1987–93 have touched all of the major islands and some points on the adjacent mainland, and made collections that include mammals, birds, reptiles, amphibians, and plants.

Like other systems of small islands, the Bocas islands have depauperate faunas and floras. Although most of the islands are very close to the mainland, small in size, and young in origin, the inventories have revealed relict taxa and morphological differentiation of taxa between islands and mainland, as well as between the islands themselves (e.g., HANDLEY 1959a). This is of special interest, as it raises an essential question: Why is there large scale response to small scale isolation? Comparative studies of species assemblages occurring on the mainland and on the islands will reveal part of the answer. Here we describe a new species of bat, genus *Artibeus*, which is found only on Isla Escudo de Veraguas, Panamá.

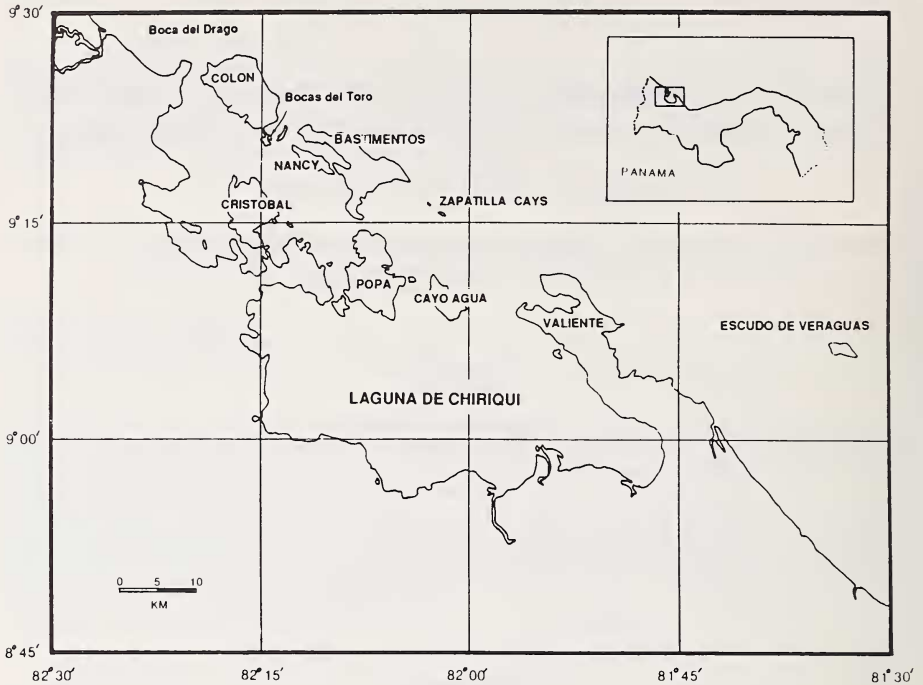


Fig. 1. Archipelago of Laguna de Chiriquí, Bocas del Toro, Panamá

Material and methods

Study area

Escudo is a small (4.3 km²), triangular, heavily forested island in the Caribbean, 17.6 km off the mainland Península Valiente. From a distance Escudo appears to be flat but, except for red mangrove (*Rhizophora*) swamps at eastern and western extremes, its surface is washboard-like. Its topography consists of a symmetrical series of low (< 50 m), steep-sided, flat-topped, parallel ridges separated by small, narrow swamps.

Escudo is the most remote of the Bocas islands. MERRILL VARN and CHARLES HANDLEY (unpubl. studies) have found it to be the oldest, formed by rising sea level. VARN and HANDLEY correlated ocean floor topography around Escudo with dates from pollen and coral cores from the western Caribbean (e.g., BARTLETT and BARGHOORN 1973). Their studies show that until sea level had risen to about 29 m below present sea level (about 9000 years before present, B. P.) Escudo was part of the mainland.

As sea level continued to rise, isolation of Escudo proceeded rapidly. Within 500 years (about 8500 years B. P.), at a sea level 25 m lower than present, the seaway between Escudo and the mainland had already opened to about 3 km. Within another 700 years (about 7200 years B. P.) sea level had risen to 15 m below present, and the distance between Escudo and the mainland had widened rapidly to about 12 km. Thereafter, the channel gained width gradually to its present 17.5 km.

Weather conditions

Frequent storms, accompanied by high winds and high tides, dominate the weather of Escudo. Distinct rainy seasons, June–August and November–December, are punctuated by indistinct dry seasons. Rainfall records have not been kept on Escudo, but because it is further away from the high mountains of the mainland, Escudo probably has less rain annually than the 2900 to 3200 mm recorded on the islands that lie within Laguna de Chiriquí.

Habitats

Evergreen forest covers about 95% of Escudo. Less than 5% of the island is currently cleared for houses, garden plots, plantains, and coconuts. Much of the forest is old growth, but tall young forest reveals that the western end of the island was extensively cleared in the recent past. All of the forest has been much damaged by wind, forming a peculiar natural mosaic of old and young growth.

Collections

HANDLEY and F. M. GREENWELL explored the southwestern sector of Escudo 19–24 March 1962, and collected among other mammals two species of bats, *Glossophaga soricina* (a nectar-feeder/insectivore) and specimens of a small canopy-foraging fruit bat resembling *Artibeus watsoni*, but larger. Again in 1990 (29 March–2 April), HANDLEY and GREENWELL surveyed the eastern quarter of Escudo. They mist netted many of the *Artibeus watsoni*-like bats and to the known chiropteran fauna they added a short-tailed fruit bat, *Carollia brevicauda*, which feeds on the fruits of shrubs.

During the last two weeks of March 1991, from a camp with indigenous people on the west shore, HANDLEY and PENNY NELSON collected bats in the western third of Escudo. They extended the series of *Artibeus watsoni*-like bats and added three more species of bats to the known fauna: *Saccopteryx leptura* and *Myotis riparius*, both insectivorous and feeding on the wing, and another small insectivorous bat, *Micronycteris megalotis*, which mainly gleans insect prey from surfaces. In April 1993 KALKO and HANDLEY stayed in a camp of native fishermen on the northeastern shore of Escudo to net and photograph the *Artibeus watsoni*-like bat. To date the native mammalian fauna of Escudo is known to include six species of bats, a marsupial, a sloth, and one rodent. In addition there are feral introduced house rats, house cats, and swine.

Specimens examined

Artibeus (new species), total 61. Panamá, Bocas del Toro: Isla Escudo de Veraguas (61).

Artibeus watsoni, total 134. Panamá, Bocas del Toro: Cayo Agua (12); Cayo Nancy (14); Cayo Zapatilla Este (3); Isla Bastimentos, Punta Vieja (9); Isla Colón, La Gruta (7); Isla Popa, 1 km SE Canal de Isla Deer (11); Isla San Cristóbal, Bocorito (21); Península Valiente (various localities around the shores of Bahía Azul) (13); Tierra Oscura, 3.5 km S Cayo Tigre (8). Panamá, Chiriquí: Progreso, 1.6 km SW, 12.8 km SE, and 24.2 km SE (34); Puerto Armuelles, 3.2 km SW (2). Specimens representative of each taxon from each locality have been returned to Panamá. All specimens mentioned in the text are in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC.

Morphometrics

External and cranial dimensions were measured in millimeters; mass in grams. Total length, ear, wingspan, and mass were measured on fresh specimens in the field. Forearm, hind foot, tibia, and calcar were measured on dry skins of prepared specimens. External measurements were taken in the conventional manner (HANDLEY 1988). Cranial measurements (Fig. 2) were taken as follows (a redefinition of the measurements first described in HANDLEY [1959b], and subsequently widely used as a standard for bats):

Greatest length: Distance between the anteriormost point of the premaxillae and the hindmost point of the skull.

Zygomatic breadth: Greatest breadth between the outer edges of the zygomata.

Postorbital breadth: Least breadth across the constriction of the frontals, posterior to the postorbital processes or bulges.

Braincase breadth: Greatest breadth of the globular part of the braincase; measured by closing the calipers on the outer walls of the braincase and sliding down to the point of abrupt flare to the squamosal edge.

Braincase depth: Greatest distance between the medio-ventral surface of the basioccipital and the dorsalmost point of the braincase, the sagittal crest not included.

Maxillary toothrow length: Greatest crown length from the anteriormost edge of the canine to the posteriormost edge of the last molar in a maxillary toothrow.

Postpalatal length: Distance between the anteriormost point of the mesopterygoid fossa (disregarding a median projection) and the anteriormost point of the foramen magnum.

Maxillary breadth: Greatest alveolar breadth between the outer edges of the maxillary toothrows.

Canine breadth: Greatest distance between outer sides of upper canines at the alveoli.

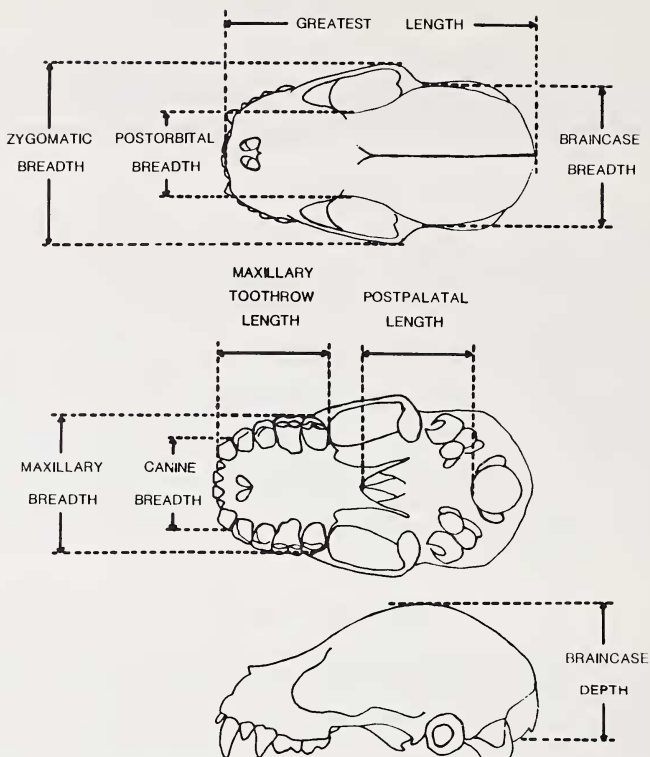


Fig. 2. Dorsal, ventral, and lateral views of a skull of *A. incomitatus*, illustrating method of taking cranial measurements

Only measurements of adults, recognized by closure of epiphyses, are included in our tabulations. As no sexual dimorphism was found, the data sets of both sexes were pooled. For mass, only males were used, as mass is variable in females.

External and cranial measurements taken in the laboratory were made with dial calipers to the nearest 0.1 mm. Data are presented as mean, \pm two standard errors. They are rounded to the nearest 1/10 for the mean and to the nearest 1/100 for the standard error. The significance of differences in measurements between the new species and the related *A. watsoni* was verified by means of the Mann-Whitney U-test. Bivariate graphs were used to compare proportions of external and cranial features of both species. Next, we assessed the morphometric variability of the specimens by examining them in multivariate space. Specifically, a Principal Components Analysis (PCA) was run, using the 15 variables listed in table 2. The Factors module of the program Systat for Windows (version 5.03; WILKINSON et al. 1992) was used for the analyses. The PCA (not rotated) was performed on a correlation matrix calculated with standardized data. To maximize the number of specimens used in the calculations, missing data were handled in a pairwise manner. That is, specimens with missing data were not automatically excluded because of a small amount of missing data during the calculation of the correlation matrix. For further discussion of the methods see WILKINSON et al. (1992), DAVIS (1986), and CHAPMAN et al. (1981).

Results

Artibeus incomitatus, new species

Holotype

USNM 579125, adult male (testis 7 × 5 mm), skin and skull, collected 19 March 1991 by CHARLES HANDLEY a meter or so above sea level, near West Point, Isla Escudo de

Veraguas, Bocas del Toro, Panamá, in a mist net in a clean coconut palm plantation. Original number, COH 17002.

Etymology

Latin, *incomitatus*, unaccompanied, alone; referring to the isolation of this bat on Isla Escudo de Veraguas, where it seems to be the only *Artibeus* and indeed the only stenodermatine.

Distribution

This bat is known only from Isla Escudo de Veraguas, province of Bocas del Toro, Panamá, where it is the most frequently netted bat. It was found in all habitats sampled, including upland forest, swamp forest, and coconut plantations. Elevational range, near sea level to 50 m, the highest point on the island.

Diagnosis

Artibeus incomitatus is characterized by large size; long, shaggy, bicolored dorsal fur; sooty dorsum; rather dark underparts; ill-defined facial stripes; cream-color on edges of ear, tragus and horseshoe; hairy posterior extremities; robust skull; broad, deeply-arched rostrum; supraorbital swelling not breaking supraorbital outline; capsulelike swellings on orbital wall always five, distinct, and subequal; subparallel zygomata; U-shaped anterior margin of mesopterygoid fossa; ill-defined inner edge of pterygoid fossa; equal or subequal cusps on I1; notches on hind edge of P4 few and indistinct; distance between paracone and protocone greater than distance between paracone and metacone on M1; paraconid cusp of m2 large, high, and situated on medial anterior edge of tooth; metaconid cusp of m2 inset from lingual margin; conulid between metaconid and entoconid of m2 large; m3 variably present or absent.

Description

Size large (forearm \bar{x} = 42.7 mm, wingspread \bar{x} = 327.0 mm, male mass \bar{x} = 13.0 g). Dorsum varying from sooty to brown, average near Burnt Umber (capitalized color terms are from RIDGWAY 1912); underparts paler, near Warm Sepia; facial stripes usually poorly defined, whitish, but sometimes well defined, white; face, between stripes, black; membranes, ears, and noseleaf blackish; ear, tragus, and sometimes horseshoe of noseleaf narrowly edged with cream; lower edge of horseshoe free; wing attached to side of metatarsus; tibia, foot, and interfemoral membrane usually appear hairy.

Skull large (greatest length \bar{x} = 20.9 mm, maxillary tooththrow \bar{x} = 7.0 mm); rostrum broad, deep, and arched, with prominent supraorbital swelling which does not break supraorbital outline; preorbital-supraorbital rim sharp-edged but low, disappearing before reaching ill-defined postorbital process; frontal wall of orbit rippled with the outlines of five well-defined, oblong, subequal capsules; postorbital constriction scarcely narrower than distance between postorbital processes; braincase narrow and deep, with evenly convex dorsal profile and low, sharp-edged sagittal crest, only vaguely connected anteriorly to postorbital processes; lambdoidal crest low and ill-defined in spots; zygomata weak and subparallel; palate wide, subcircular, with well-marked lateral depressions between canine and M1; postpalatal extension parallel-sided, with U-shaped posterior margin; pterygoid fossa with ill-defined inner edge, opening diagonally inward; basal pits (interauricular depressions) deep and well-defined, with rounded median septum; auditory bullae small.

Tooth formula I 2/2, C 1/1, P 2/2, M 2/2-3 X 2 = 28-30. I1 with equal or subequal cusps; notches on hind edge of blade of P4 usually few and indistinct; M1 wide, with both protocone and hypocone expanded and distance between paracone and protocone consid-

erably greater than distance between paracone and metacone; lingual longitudinal sulcus on p4 deep, extending to near base of tooth; anterolingual (paraconid) cusp of m2 large and displaced medially from lingual margin of tooth to form, with the anterolabial (protoconid) cusp, an anterior rim for the tooth (see Fig. 3 for nomenclature of cusps); conulid between metaconid and entoconid somewhat enlarged; m3 tiny, often lacking from one or both mandibles.

Measurements of the holotype

Adult male: Total length 59 mm, tail vertebrae 0 mm, hind foot (dry) 11 mm, ear from notch 17 mm, forearm 42.4 mm, wingspread 325 mm, tibia 15.2 mm, calcar 4.2 mm, mass 12.5 g. Greatest length of skull 20.6 mm, zygomatic breadth 11.7 mm, postorbital breadth 5.1 mm, braincase breadth 8.8 mm, braincase depth 7.7 mm, maxillary toothrow length 7.1 mm, postpalatal length 6.8 mm, maxillary breadth 8.5 mm, canine breadth 5.5 mm. See table 1 for a summary of measurements of a series.

Comparisons with related species

Compared with its close relative, *A. watsoni* of the Bocas islands and mainland, *A. incommitatus* averages 15% greater in mass, 10% larger in external dimensions, and 6% larger in cranial dimensions. Every measurement except braincase depth is significantly

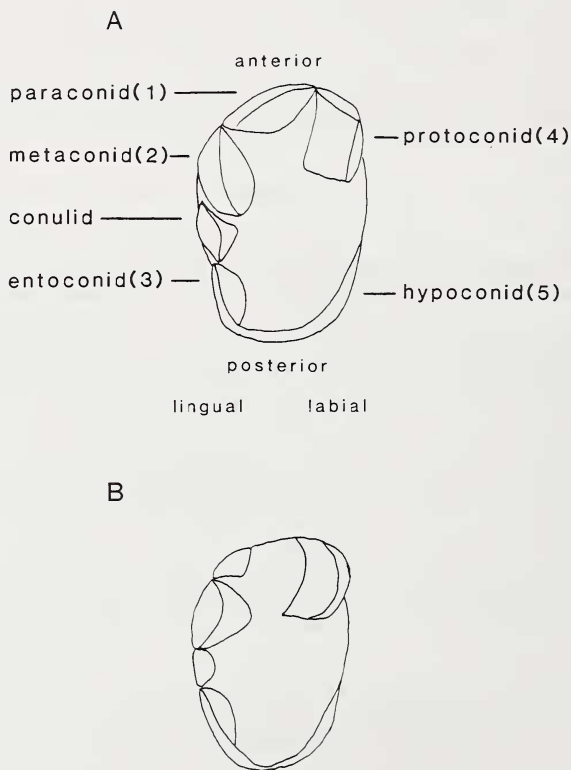


Fig. 3. Occlusal view of lower second molar (schematic drawings based on camera lucida sketches). A: *A. incommitatus* from Isla Escudo de Veraguas. B: *A. watsoni* of Península Valiente. Names of cusps are from HANDLEY (1959b); numbers of cusps are from ANDERSEN (1908)

larger in *A. incomitatus* ($p < 0.001$, Mann-Whitney U-test). Relative to *A. watsoni*, the largest measurements are tibia and calcar; the smallest are hind foot, zygomatic breadth, braincase breadth, and braincase depth. Bivariate scatter graphs of all individuals measured illustrate very well the high degree of separation between the two taxa. Figure 4 shows a pair of external characters; figure 5, cranial characters.

Further, the Principal Components Analysis (PCA) confirmed the large size difference between *A. incomitatus* and *A. watsoni*. The results of the PCA are summarized in tables 2 and 3, and figures 6 and 7. Fifteen components (PCs) were derived but only the first two axes had eigenvalues greater than 1; i.e. they represent more variance than any single variable.

PC-I accounted for almost 59% of the variation in the data and is a classic size axis, indicated by the high positive loadings of all the variables (Tab. 2). This is very frequently the case in morphometric studies on single or closely related taxa (see CHAPMAN et al. 1981). The loadings also indicate that of the original variables, greatest length is the best indicator of overall size (loading = 0.95) and braincase depth and postpalatal length are the least effective (both with loadings of approx. 0.55). The scores for the specimens (sample averages in table 3; scores plotted figures 6 and 7) give an indication of the overall size of the specimens, based on input from all 15 variables. A specimen with a high positive value for PC-I is very large compared to those with values near zero. Those with high negative values are the smallest (see CHAPMAN et al. 1981).

PC-II accounted for just over 8% of the variance in the data matrix and represents shape variation in braincase size (positive; braincase breadth and depth and ear versus selected standard lengths) (negative; total length, hindfoot, postpalatal length, tibia, and calcar). Not surprisingly, these variables tested to have the smallest loadings on PC-I. A specimen with a high positive value on this axis has a relatively large braincase and ear measurement and is relatively smaller in the length measurements. A high negative value would indicate the opposite.

In order to interpret these results we examined the scores; that is, how the specimens related to the new axes; and analyzed patterns in them relative to sex, taxon, and sample. No apparent trends could be discerned related to sex on either axis, suggesting that sexual dimorphism is not significant in these taxa.

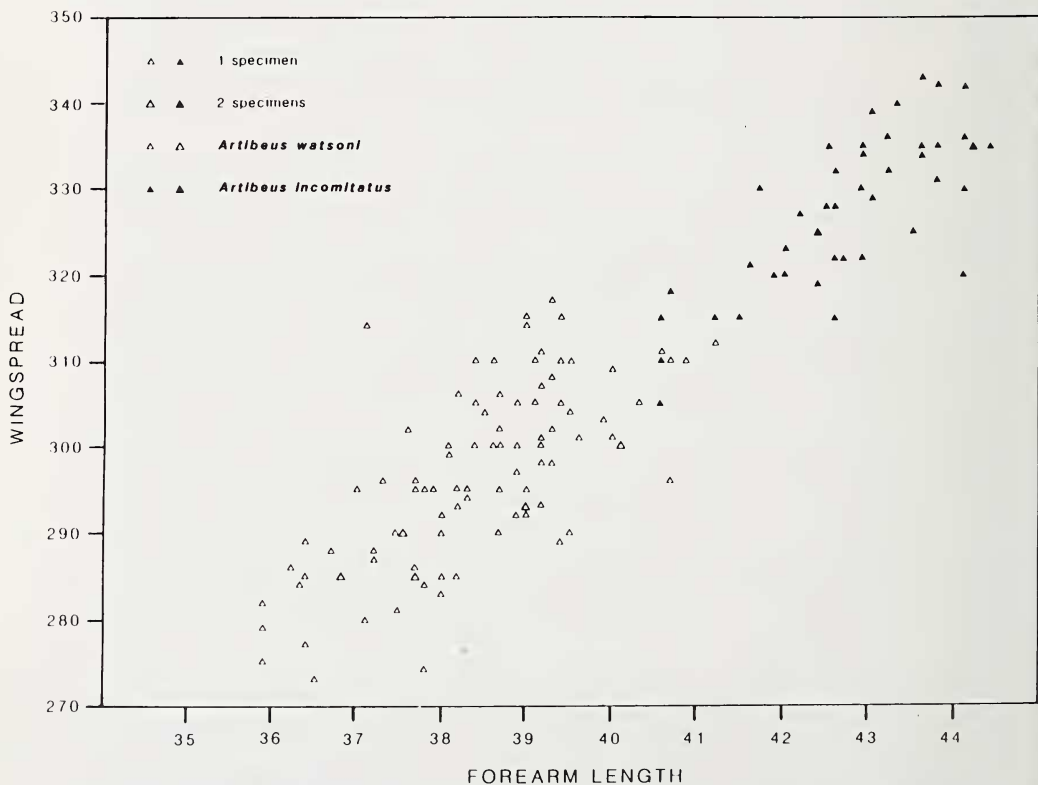
Plotting the scores with the data coded to represent the specimens of each population (PC-I) indicate clear differences between *A. watsoni* and *A. incomitatus*. In PC-I, the specimens from Isla Escudo all plot positive, some highly positive, with relatively little overlap with the other samples (Fig. 6). This reflects the large size difference described for *A. incomitatus* relative to the much smaller *A. watsoni*. Plotting the average scores for each population shows trends for PC-II which are more subtle but still apparent (Fig. 7). Ignoring the Isla Escudo specimens and concentrating on *A. watsoni* alone, we see a mainland-island trend in the average values for PC-II. The Chiriquí specimens not only tend to be small but they tend to have larger negative values for PC-II, indicating that they have relatively high values for the length measurements and small values for the braincase and ear measurements. On the other side of the PC-II trend are the larger near-shore islands of Colón and Bastimentos. Most other islands and Península Valiente are intermediate but closer to the larger islands. Isla San Cristóbal and Tierra Oscura, on the adjacent mainland, plot more toward the middle area. This suggests a northeast (island) – southwest (mainland) cline.

Dorsal coloration is similar in *A. incomitatus* and *A. watsoni*, but underparts are darker, gray-brown rather than buffy, in *A. incomitatus* (12 of 13 Península Valiente specimens are paler than the average Escudo specimen; only 6 of 45 Escudo specimens are as pale as the average Valiente specimen). Less than half (44%) of Escudo specimens have prominent well-defined, white facial stripes, while more than two-thirds (69%) of Valiente *A. watsoni* have prominent stripes. *A. incomitatus* usually (75%) appears to have posterior

Table 1. Measurements of adult *Artibeus*

Except for mass, which is for males only, measurements are for females and males combined. Each

Total length (mm)	Hind foot (dry) (mm)	Ear (mm)	Forearm (mm)	Tibia (mm)	Calcar (mm)	Wingspan (mm)	Mass (g)
<i>Artibeus incommitatus</i> , Isla Escudo de Veraguas							
59.7±0.61	11.1±0.16	17.7±0.14	42.7±0.30	14.7±0.15	5.0±0.13	327.0±2.30	13.0±0.34
55-64	10-13	17-19	40.6-44.4	13.6-15.8	4.0-5.9	305-343	10.8-16.0
(60)	(49)	(60)	(48)	(48)	(48)	(57)	(50)
<i>Artibeus watsoni</i> , Peninsula Valiente							
53.7±2.1	10.1±0.26	16.6±0.46	38.4±0.8	13.3±0.38	4.2±0.16	298.3±5.44	10.9±0.72
46-60	9-11	15-18	35.9-40.7	12.4-14.7	3.4-4.5	282-310	9.5-13.0
(13)	(13)	(13)	(13)	(13)	(13)	(13)	(19)
<i>Artibeus watsoni</i> , Cayo Nancy							
54.1±0.96	10.6±0.26	16.1±0.51	38.0±0.58	13.3±0.50	4.4±0.20	294.6±6.00	11.3±0.62
52-59	10-11	14-17	35.9-39.2	12.2-14.9	3.8-5.1	277-315	9.5-13.0
(14)	(14)	(14)	(14)	(14)	(14)	(14)	(10)
<i>Artibeus watsoni</i> , all islands (except Escudo) and mainland							
54.5±0.65	10.4±0.10	16.0±0.25	38.5±0.25	13.0±0.14	4.4±0.07	296.6±2.10	11.1±0.27
42-60	9-12	12-18	35.9-41.6	11.3-14.9	3.4-5.4	273-317	9.0-14.0
(96)	(98)	(97)	(98)	(98)	(96)	(96)	(77)

Fig. 4. Comparison of wingspread and forearm length in 45 specimens of *A. incommitatus* from Isla Escudo de Veraguas and 96 specimens of *A. watsoni* from shores and islands of Laguna de Chiriquí

incomitatus and *A. watsoni*

measurement is given as the mean \pm 2 standard errors, Min/Max and the number of specimens measured

Greatest length (mm)	Zygomatic breadth (mm)	Postorbital breadth (mm)	Braincase breadth (mm)	Braincase depth (mm)	Maxillary tooththrow (mm)	Postpalatal length (mm)	Maxillary breadth (mm)	Canine breadth (mm)
20.9 \pm 0.10 20.0–21.7 (60)	12.1 \pm 0.07 11.3–12.8 (58)	5.0 \pm 0.04 4.7–5.3 (60)	9.2 \pm 0.05 8.8–9.6 (60)	7.6 \pm 0.06 7.1–8.1 (59)	7.0 \pm 0.04 6.7–7.4 (60)	6.8 \pm 0.06 6.3–7.3 (57)	8.6 \pm 0.6 8.0–9.2 (60)	5.6 \pm 0.04 5.3–5.9 (60)
19.7 \pm 0.27 19.1–20.6 (13)	11.4 \pm 0.25 10.6–12.4 (13)	4.8 \pm 0.10 4.4–5.1 (13)	8.8 \pm 0.11 8.5–9.2 (13)	7.6 \pm 0.11 7.1–8.0 (13)	6.5 \pm 0.13 6.2–6.9 (13)	6.4 \pm 0.13 6.0–7.0 (13)	8.1 \pm 0.17 7.6–8.8 (13)	5.2 \pm 0.10 4.9–5.5 (13)
19.5 \pm 0.19 19.1–20.1 (11)	11.6 \pm 0.17 11.1–12.4 (13)	4.7 \pm 0.06 4.5–4.9 (13)	8.9 \pm 0.13 8.4–9.3 (13)	7.5 \pm 0.13 7.1–7.8 (10)	6.5 \pm 0.09 6.1–6.7 (13)	6.3 \pm 0.10 6.1–6.7 (11)	8.0 \pm 0.17 7.4–8.4 (12)	5.2 \pm 0.12 4.8–5.5 (12)
19.6 \pm 0.08 18.7–20.6 (94)	11.6 \pm 0.07 10.6–12.4 (91)	4.7 \pm 0.03 4.3–5.1 (96)	8.8 \pm 0.04 8.3–9.3 (96)	7.5 \pm 0.05 7.0–8.2 (93)	6.5 \pm 0.04 6.1–6.9 (97)	6.4 \pm 0.05 5.9–7.2 (93)	8.1 \pm 0.05 7.4–8.8 (95)	5.3 \pm 0.04 4.8–5.7 (95)

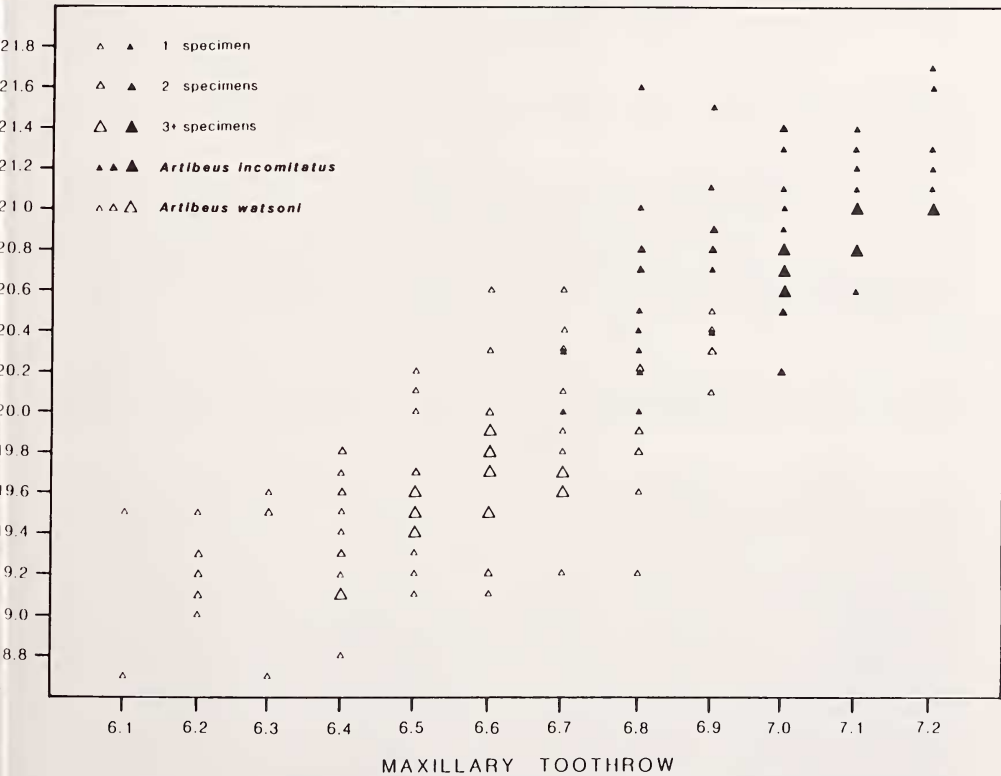


Fig. 5. Comparison of greatest length of skull and maxillary tooththrow length in 60 specimens of *A. incomitatus* from Isla Escudo de Veraguas and 94 specimens of *A. watsoni* from shores and islands of Laguna de Chiriquí

Table 2. Variables used in Principal Components Analysis and their loadings for the first two Principal Components

Eigenvalues and percent variance explained for first two Principal Components, are also tabulated

Variables	Loadings	
	PC-I	PC-II
Total length	0.6674	-0.4435
Hind foot	0.6288	-0.3199
Ear	0.7035	0.2067
Forearm	0.8839	-0.1481
Greatest length	0.9499	0.0583
Zygomatic breadth	0.8525	0.1941
Postorbital breadth	0.7235	-0.0401
Braincase breadth	0.8155	0.3313
Braincase depth	0.5509	0.6081
Maxillary toothrow	0.8946	0.1222
Postpalatal length	0.5485	-0.3666
Maxillary breadth	0.8696	0.1430
Canine breadth	0.8351	0.0499
Tibia	0.8050	-0.2376
Calcar	0.6107	-0.3233
Eigenvalue (Total = 15)	8.8138	1.2193
1 % Variance explained	58.7589	8.1287

extremities (tibia, foot, and interfemoral membrane) hairy, whereas *A. watsoni* appears to have these parts almost naked (12 of 13 specimens from Península Valiente). Under magnification all specimens of both species prove to have hairy posterior extremities. Hairs are longer and possibly denser in *A. incomitatus*.

The skull of *A. incomitatus* is heavier and more bulky than the skull of *A. watsoni*. Supraorbital swelling is pronounced, but usually not sufficiently in Escudo specimens (23 of 30) to break the smooth-edged supraorbital outline, whereas only 11 of 30 *A. watsoni* have the outline unbroken. Capsule-like swellings on the frontal wall of the orbit always five, distinct, and subequal in *A. incomitatus*, sometimes only four, often indistinct, and always variable in size in *A. watsoni*. Zygomata usually subparallel (18 of 30) in Escudo specimens, but almost always (26 of 30) narrow anteriorly and swept-back in *A. watsoni*. Anterior margin of mesopterygoid fossa almost always (26 of 30) U-shaped in *A.*

incomitatus, often V-shaped in *A. watsoni* (17 of 30). Inner edge of pterygoid fossa always ridged in *A. watsoni*, but ridge almost always (26 of 30) ill-defined or absent in *A. incomitatus*.

Cusps of I1 almost always (39 of 42) equal or subequal in *A. incomitatus*, while the outer cusp usually (30 of 44) is larger in *A. watsoni*. Notches on the hind edge of the blade of P4 usually few and indistinct in Escudo specimens (29 % with one sharp notch, 62 % with 1-3 obscure notches, and 9 % notchless), whereas 56 % of Valiente specimens have 1-3 sharp notches and 44 % have 1-3 obscure notches. The paraconid cusp of m2 has a medial location on the anterior edge of the tooth in 29 of 35 specimens of *A. incomitatus*, a

Table 3. Statistics for scores from Principal Components Analysis of samples of *Artibeus incomitatus* from Isla Escudo de Veraguas and *A. watsoni* from ten localities in Bocas del Toro and Chiriquí, Panamá

Localities	Abbrev. for Locality	N	Factor Score Data	
			PC-I Mean/S.E.	PC-II Mean/S.E.
Isla Escudo	E	45	1.31/0.07	-0.43/0.14
Península Valiente	V	13	-0.47/0.19	0.88/0.19
Isla Colón	C	4	-0.03/0.62	1.21/0.19
Isla Bastimentos	B	8	-0.54/0.21	1.30/0.35
Cayo Nancy	N	9	-0.44/0.18	0.27/0.29
Cayo Zapatilla Este	Z	3	-0.51/0.43	0.79/0.40
Cayo Agua	A	11	-0.78/0.13	0.36/0.26
Isla Popa	P	11	-0.32/0.09	0.22/0.22
Isla San Christóbal	S	16	-0.30/0.10	0.08/0.18
Tierra Oscura	T	7	-0.56/0.14	-0.21/0.23
Progreso, Chiriquí	Q	13	-0.98/0.09	-1.00/0.17

**Principal Components Analysis
Scores for Specimens**

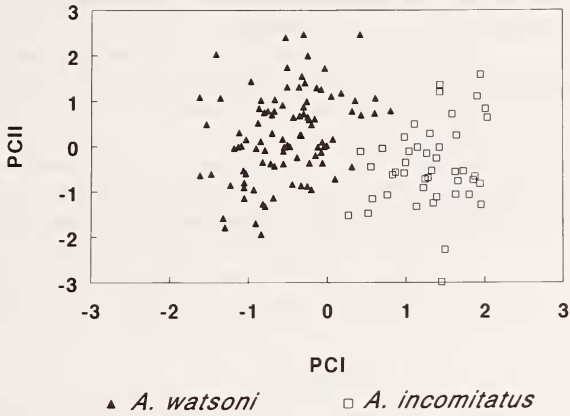


Fig. 6. Results of Principal Components Analysis. Scores of specimens plotted for PC-I (X-axis) versus PC-II. Labels indicate species of specimen; triangle = *Artibeus watsoni*; square = *Artibeus incomitatus*

**Principal Components Analysis
Sample Average Scores**

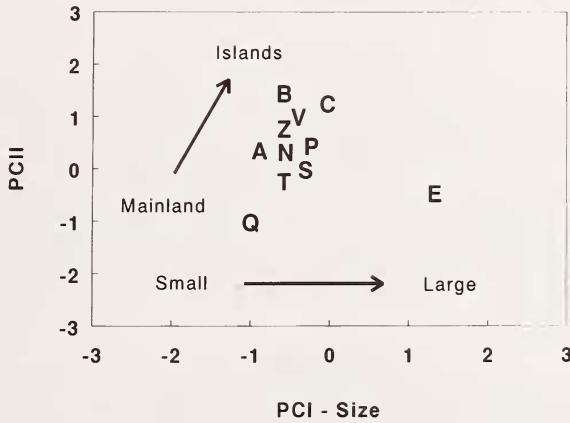


Fig. 7. Results of Principal Components Analysis. Scores of specimens plotted for PC-I (X-axis) versus PC-II. Labels are mean values for populations (see Tab. 3)

lateral location in 45 of 46 specimens of *A. watsoni* (Fig. 2). This cusp is large (24 of 35) and high (18 of 35) in *A. incomitatus*, but small (42 of 46) and low (34 of 46) in *A. watsoni*. The metaconid cusp of m2 is inset from the lingual margin of the tooth in 22 of 35 specimens from Escudo, but is on the margin of the tooth in 41 of 46 *A. watsoni*. The conulid between the metaconid and entoconid cusps of m2 is large in 28 of 35 *A. incomitatus*, but in only 13 of 46 *A. watsoni*. Presence or absence of m3 on either mandible varies among populations of these bats, from a frequency of zero on Cayo Zapatilla Este and 0.5 on Cayo Nancy to 1.7 on Isla Popa and 2.0 on Isla Colón. The mean for Isla Escudo is 1.2 and the mean for the other islands and mainland of Bocas del Toro collectively is 1.5.

There is another small species of *Artibeus* (*A. phaeotis*), on the mainland and on some of the islands of Bocas del Toro. Compared with *A. incommitatus*, it is smaller, in the size range of *A. watsoni*; dorsal fur distinctly tricolor versus bicolor or indistinctly tricolor, shorter (6 mm versus 8 mm), smooth-lying rather than shaggy, and brownish rather than sooty; underparts more buffy; facial stripes pure white and sharply defined; margins of ears, tragus, and sometimes noseleaf yellow or orange rather than creamcolor. Rostrum shorter, shallower, flatter, and less arched; supraorbital not swollen; postorbital constriction narrower; braincase deeper and wider; zygomatic taper (narrow anteriorly, flaring posteriorly); palate shorter and broader, subcircular; lateral palatal depressions usually ill-defined or absent; anterior edge of mesopterygoid fossa V-shaped; inner edge of pterygoid fossa sharply ridged, constricting roof of mesopterygoid fossa, and causing pterygoid fossa to open posteriorly rather than inward. Protocone of M1 relatively closer to metacone, so that protocone, metacone, and paracone usually come close to forming an equilateral triangle; m2 longer and narrower, but otherwise like m2 of *A. watsoni*; m3 always absent.

Remarks

To check for the possibility that *A. watsoni* as well as *A. incommitatus* might occur on Escudo, during the 1991 expedition to Escudo HANDLEY selectively collected the smallest *Artibeus* that were netted. This skewed the *A. incommitatus* series toward the small side, but did not turn up any specimens in the size range or with morphological characters of *A. watsoni*. Actually, there is surprisingly little variation, considering the size of the series (159 specimens), among the skulls from Escudo on the one hand and those from all other islands and mainland on the other (Tab. 1; Figs. 4, 5).

Ectoparasites

Parasitic flies (Streblidae) collected by HANDLEY and NELSON from *A. incommitatus* on Isla Escudo prove to represent a well-differentiated undescribed species, apparently evolved from *Paratrichobius lowei* Wenzel, a parasite of *A. watsoni* (R. V. PETERSON, unpubl. results). *P. lowei* has been reported from *A. watsoni* taken in eastern Panamá (San Blas and Darién) (WENZEL et al. 1966) and from "*Artibeus cinereus*" taken in Venezuela (Bolívar) (WENZEL 1976). The Venezuelan hosts have been reidentified as *Artibeus glaucus bogotensis*, a member of the *A. glaucus* group, which also includes *A. watsoni* (HANDLEY 1987).

Discussion

Taxonomic status of *A. incommitatus*

Insular populations of organisms showing morphological differentiation from mainland taxa pose taxonomic problems in interpreting the observed variability. As summarized by WILSON (1991), differentiated island populations can depending on the conceptual viewpoint of the researcher be regarded either as subspecies of mainland species or as endemic island species.

Because geographic isolation interrupts or diminishes gene flow between populations, it represents one of the most important factors promoting speciation. However, assessing whether spatial isolation on an island has been sufficient to produce reproductive isolation, the basic criterion of the biological species concept, remains an imponderable problem always confounding systematic studies of island organisms. Often this question can be addressed only indirectly.

Ideally, information about formation of the island, degree and duration of isolation

from the mainland, detailed studies on morphological and genetic variability of island and mainland populations, as well as studies of ecological (e.g., community structure), behavioral, and physiological characteristics should be available to allow a taxonomist to judge adequately the significance of observed differences between island and mainland populations. In reality such information seldom is available.

In our study we have described *A. incomitatus* as a species endemic on Isla Escudo de Veraguas, Panamá. We compared it with a similar species, *A. watsoni*, which is widespread on the mainland from southern México to Ecuador (HALL 1981). Based on a set of morphological characteristics shared by the two taxa we assume that *A. incomitatus* and *A. watsoni* have evolved from a common ancestor. We further assume that the characters which distinguish *A. incomitatus* and *A. watsoni* were variable in the ancestral bat before Isla Escudo de Veraguas was isolated. After isolation the characters were variously accentuated in the evolving *A. incomitatus* and *A. watsoni*.

For several reasons we regard *A. incomitatus* and *A. watsoni* as species rather than as subspecies. First, there is the matter of scale, a commonly used criterion for ranking insular populations. If differentiation of the organism on an island is greater than differentiation between contiguous populations on the mainland which are supposed to be geographic variants, then the insular population should be regarded as a species. *A. watsoni* is regarded as monotypic throughout its range (HALL 1981), but actually it is geographically variable (HANDLEY 1987; unpubl. results). However, the degree of difference is much greater between the insular *A. incomitatus* and the mainland *A. watsoni* than between any of the mainland populations of *A. watsoni*. There is no evidence of intergradation between the taxa, and every external and cranial dimension we measured, except cranial breadth, is significantly larger in *A. incomitatus*.

Principal Components Analysis confirms the great size difference apparent in the Escudo specimens. It also indicates an interesting trend, from the mainland across the inner islands of Laguna de Chiriquí, in both shape and size of skull that invites further study, especially documentation of genetic relationships of the samples. The results could demonstrate a morpho-genetic cline, indicating a species in the process of spinning off from a sister species, or show the progressive fragmentation of a species-range, with the predictable effect of isolating various populations.

However, molecular analysis alone, which is increasingly used to determine phylogeny and taxonomic status of organisms, is not necessarily the solution to the species dilemma. For example, recent studies on Peruvian *Sturnira* (Phyllostomidae) led to conflicting evidence in morphological and genetic characters (PACHECO and PATTERSON 1992). Some of the morphological characters did not show in the genetic analysis and, in reverse, some molecular differences did not show in morphology.

Second, in addition to statistical differences in external and cranial measurements, *A. incomitatus* and *A. watsoni* differ also in numerous discrete morphological characters in the dentition, cranium, and pelage. Among the dental characters that distinguish *A. incomitatus* the one we consider to be the most significant involves the size, shape, and location of cusps on the second lower molar. The placement of the paraconid in *A. incomitatus* on the anterior margin of the tooth, close to the protoconid, has the effect of giving the tooth a substantial anterior rim, undeveloped in *A. watsoni*. In contrast, *A. watsoni* almost always has a wide, low gap between the paraconid and the protoconid. These differences in dentition must give the teeth of the two species slightly different functional characteristics, which remain to be explained. The most distinctive cranial feature of the Escudo bat is suppression of the ridge at the inner edge of the pterygoid fossa. In pelage, *A. incomitatus* is characterized by drabness: sooty dorsal coloration, darkening of the underparts, and obsolescence of facial stripes, only to a limited extent seen in the mainland bat.

Third, the host-specific parasitic streblid fly of *A. incomitatus* has differentiated to the species level from the ancestral fly on *A. watsoni*. Assuming that the coevolution in host

and parasite proceeds at a similar rate this evidence also supports the specific status of *A. incomitatus*.

Fourth, long-term studies of *A. watsoni* in Isla Barro Colorado Island (BCI), a field station of the Smithsonian Tropical Research Institute, Panamá, suggest that this bat, and presumably also *A. incomitatus*, have very small home ranges, thus further enforcing the isolation of mainland and island populations. On this small (1500 ha, 5 × 5 km) island in Gatun Lake (Panamá Canal), 40 marked *A. watsoni* were recaptured up to three times during a five year interval. Most individuals (36) were recaptured within 1 km of their mark sites, more than 50% of them (22) at the original mark site. The greatest recorded movement was only 3 km. The only movement over water probably was no more than 200 m. Furthermore, the wing morphology of *A. incomitatus* and *A. watsoni* makes it highly unlikely that either could commute between the mainland and Escudo. Both have rather short, broad wings typical of most stenodermatine bats. This wing shape adapts them for slow, maneuverable flight in and around vegetation but constrains them from sustained flight over long distances (NORBERG and RAYNER 1987). Moreover, the frequent storms around Escudo would further limit movement between mainland and island.

Evolution on Escudo

The isolation of Escudo limits immigration and facilitates evolution. Escudo is more isolated than any other island of Bocas del Toro. On it *A. incomitatus* has differentiated to the species level. On the other islands, which are much closer to the mainland, populations of *A. watsoni* are barely distinguishable from those of the mainland.

Seven of the nine species of native mammals of Escudo are differentiating from their mainland counterparts. *Artibeus incomitatus*, *Glossophaga soricina*, *Miconycteris megalotis*, and *Hoplomys gymnurus* are larger; *Caluromys derbianus*, *Carollia brevicauda*, and *Bradypus variegatus* are smaller. Only the aerial insectivorous bats, *Saccopteryx leptura* and *Myotis riparius*, seem to be morphologically unchanged. Some of the birds of Escudo clearly are isolated and have undergone morphological differentiation. The hummingbird (*Amazilia handleyi*), manakin (*Manacus amittinus*), and wren (*Thryothorus nigricapillus*) are strikingly larger and more colourful than their mainland congeners, near the species level of differentiation. The blue tanager (*Thraupis episcopis*) is less differentiated and may be a later immigrant, or may be evolving more slowly. S. L. OLSON (pers. comm.) has found the rail, kingfisher, pigeon, parrot, flycatchers, and warbler of Escudo to be little if any differentiated. Among the resident land birds, at least the pigeon and parrot may fly periodically to the mainland.

Escudo has existed at most only about 9000 years, but once established, the channel separating it from the mainland widened rapidly and the sedentary nature of the *Artibeus* insured its quick isolation from parental populations on the receding mainland. Although 9000 years appears to be little time for speciation there are other examples in mammals. BERGSTROM and HOFFMAN (1991) have inferred for example that the most recent cycle of differentiation and speciation in chipmunks (*Tamias*) in the montane islands in the Great Basin and southern Rocky Mountains of the southwestern United States has occurred in the 10,000 years since the Pleistocene (see also PATTERSON 1982).

Factors leading to evolution and extinction on Escudo

We assume that all of the mammals of Escudo may be survivors of selective extinction from a species-rich mainland fauna following the fragmentation of Escudo. The inner islands, closer to the mainland, harbor more species. With increasing distance from the mainland the number of species declines. Extinction is rapid and extensive on small islands, leading

soon to diminished resource and habitat diversity and consequently to reduced faunal diversity.

Compared with their mainland counterparts, island populations of animals often undergo significant changes in body size. Smaller animals tend to increase in size whereas larger animals tend to decrease in size (e.g. CASE 1978; HEANEY 1978; LAWLOR 1982; LOMOLINO 1985). On the Bocas islands we have found both phenomena – dwarfism and gigantism. For example the agouti (*Dasyprocta*), long-nosed armadillo (*Dasypus*), and sloths (*Bradypus* and *Choloepus*) on the islands are smaller than their mainland congeners whereas some rodents (e.g., *Tylomys*) are larger (HANDLEY, unpubl. results). A number of hypotheses, including resource and habitat limitation, interspecific competition, and predator pressure, have been put forward to explain this pattern (for summaries see as examples ANGERBJÖRN 1985 and LOMOLINO 1985).

The factors we regard as most significant in this process on Escudo are reduction in habitat diversity and the resulting resource limitation. At first glance resource limitation would seem to contradict our observation that *A. incomitatus* is significantly larger, and has a much higher population density than its mainland counterpart, *A. watsoni*. However, whereas *A. incomitatus* is the only stenodermatine on Escudo, on the mainland and on all other islands of Bocas del Toro, *A. watsoni* and other small stenodermatines compete for fruit with larger species, often in graded series of size classes. The decrease in abundance and diversity of fruiting plants on islands is a particularly serious problem for frugivorous bats which live on a very tight energy budget and need a constant supply of fruits (HANDLEY et al. 1991; MORRISON 1980). First observations on Escudo indicate that there is insufficient food for larger bats. For example, there are few figs of any kind on Escudo, and *Ficus insipida* seems not to occur there. Throughout Panamá this species is a major food source for large numbers of fruit-eating bats ranging in mass from 8–75 g (e.g. BONACCORSO 1979; HANDLEY et al. 1991). We assume that release from interspecific competition with other frugivorous stenodermatines might have freed the evolving *A. incomitatus* to occupy a wider niche and thus to become bigger and more abundant. A larger body size would adapt it to utilize the full (although limited) range of fruit sizes available on Escudo. *A. incomitatus* may have already reached its potential maximum body size. Its size ratio of 1.17 to its mainland relative, *A. watsoni*, is comparable to means of ratios of large suits of pairs of island and mainland species compiled by LOMOLINO (1985).

Another factor pressing for larger size in *A. incomitatus* might be the reduced and seasonally variable abundance of fruit on Escudo. LINDSTEDT and BOYCE (1985) have argued that seasonality selects for larger body size, which enhances survivorship through increased fasting endurance. Larger bats tolerate hunger better than smaller bats do. Although frugivorous neotropical bats typically have little body fat (McNAB 1976) we found substantial amounts of fat in *A. incomitatus* but little or none in *A. watsoni* collected at the same season.

WILSON (1991) found similar trends in size among small mammals on the Tres Marías islands of Mexico. These islands are further from the mainland and much larger than Escudo. As on Escudo, only one stenodermatine is present (*A. intermedius koopmani*). However, *Artibeus intermedius* already is one of the largest stenodermatines, yet the island bat is still larger than mainland *A. intermedius*. Furthermore, WILSON (1991) found higher diversity in insectivorous vespertilionid bats than in the mainly frugivorous and/or nectarivorous phyllostomids. He postulated that their lower diversity might reflect unpredictability of supplies of fruit and flowers.

Acknowledgements

More than to any other person we are indebted to LIGIA PAGET of Bocas del Toro for her unfailing support and friendship. We are grateful to FRANCIS M. GREENWELL and PENNY NELSON who helped

to collect and to prepare the specimens of *A. incomitatus*. The Instituto Nacional de Recursos Naturales Renovables of Panamá (INRENARE), notably ROBERTO ARRANGO, provided collecting and export permits. MERCEDES ARROYO, ISIS IVANCIC, GLORIA MAGGIORI, and MARÍA MORELLO of the Smithsonian Tropical Research Institute (STRI) expedited administrative and logistical details. We are most grateful to ARLOINE HOOD and KERRY THOMSON who processed the specimens in the museum; MERRILL VARN for her reconstructions of prehistoric shorelines; RALPH CHAPMAN for his invaluable generosity of sharing his expertise in statistics and morphometrics with us; and DARELYN HANDLEY who prepared the table of measurements and edited the manuscript. The Escudo expeditions were financed by grants from the National Science Foundation and the National Museum of Natural History (NELSON Fund and Research Opportunities Fund), the Smithsonian Office of Products Development and Licensing, and a gift from JAMES and PAULA NELSON of Hillsboro, Oregon. E. K. V. KALKO was supported by a NATO postdoctoral fellowship. Transportation was furnished by the U.S. Army (Maj. VERNON J. TIPTON), STRI (JOHN CHRISTY, EGBERT LEIGH and DAVID WEST), United Brands, Changuinola Division (CAMERON FORSYTHE, General Manager), and Asociación Nacional para la Conservación de la Naturaleza, Panamá (ANCON).

Zusammenfassung

Evolution, Biogeographie und Beschreibung einer neuen, fruchtfressenden Fledermausart der Gattung Artibeus Leach (1821) aus Panama

Wir beschreiben und benennen eine neue, fruchtfressende Fledermausart der Gattung *Artibeus* aus den Neotropen. Die neue Art ist ein Lokalendemit und kommt nur auf der Insel Escudo de Veraguas, Panamá, vor. Escudo de Veraguas liegt in der Provinz Bocas del Toro in Nordwest-Panamá, ungefähr 18 km von der karibischen Küste entfernt. Aufgrund einer Vielzahl gemeinsamer Merkmale nehmen wir an, daß sich die neue Art aus einer *Artibeus watsoni*-nahestehenden Fledermausart entwickelt hat. *A. watsoni* ist auf dem angrenzenden Festland und auf den anderen Inseln in der Provinz Bocas del Toro weitverbreitet und häufig. Im Vergleich zu *A. watsoni* wiegt die neue Art ca. 15 % mehr, die Körperproportionen sind um ca. 10 % und die Schäeldimensionen um ca. 6 % größer. Zudem unterscheidet sich die neue Art in einer Anzahl diskreter morphologischer Merkmale, insbesondere in der Bezeichnung von *A. watsoni*. Wir diskutieren Aspekte zur Evolution und Biogeographie von *A. incomitatus* und leiten daraus Mechanismen ab, die möglicherweise zur Artbildung dieser neuen Fledermausart beigetragen haben.

Literature

- ANDERSEN, K. (1908): A monograph of the chiropteran genera *Uroderma*, *Enchisthenes*, and *Artibeus*. Proc. Zool. Soc. London, 204–319.
- ANGERBJÖRN, A. (1985): The evolution of body size in mammals on islands: some comments. Am. Nat. 125, 304–309.
- BARLETT, A. S.; BARGHOORN, E. S. (1973): Phytogeographic history of the Isthmus of Panamá during the past 12,000 years (a history of vegetation, climate, and sea-level change). In: Vegetation and vegetational history of northern Latin America. Ed. by A. GRAHAM. Amsterdam: Elsevier Scie. Publ. Co.
- BERGSTROM, B. J.–HOFFMANN, R. S. (1991): Distribution and diagnosis of three species of chipmunks (*Tamias*) in the Front Range of Colorado. The Southwestern Naturalist 36, 14–28.
- BONACCORSO, F. J. (1979): Foraging and reproductive ecology in a Panamanian bat community. Bull. Florida State Mus. Biol. Sci. 24, 359–408.
- CASE, T. J. (1987): A general explanation for insular body size trends in terrestrial vertebrates. Ecol. 59, 1–18.
- CHAMPMAN, R. E.; GALTON, P. M.; SEPkoski, J. J. Jr.; WALL, W. P. (1981): A morphometric study of the cranium of the pachycephalosaurid dinosaur *Stegoceras*. J. Paleontology 55, 608–618.
- DAVIS, J. C. (1986): Statistics and data analysis in geology. 2nd ed. New York: John Wiley.
- HALL, E. R. (1981): The mammals of North America. 2nd ed. New York: John Wiley.
- HANDLEY, C. O., Jr. (1959a): A review of the genus *Hoplomys* (Thick-spined rats), with description of a new form from Isla Escudo de Veraguas, Panamá. Smithsonian Miscell. Coll. 139, 1–10.
- (1959b): A revision of American bats of the genera *Enderma* and *Plecotus*. Proc. United States Nat. Mus. 110, 95–246.
- (1987): New species of mammals from northern South America: Fruit-eating bats, genus *Artibeus* Leach. In: Studies in Neotropical mammalogy: Essays in honor of Philip Hershkovitz. Ed. by B. D. PATTERSON and R. M. TIMM. Fieldiana: Zoology 39, 163–172.
- (1988): Specimen preparation. In: Behavioral and ecological methods for the study of bats. Ed. by T. H. KUNZ. Washington: Smithsonian Institution Press. Pp. 437–457.
- HANDLEY, C. O., Jr.; WILSON, D. E.; GARDNER, A. L. (1991): Demography and natural history of the

- common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panamá. *Smithsonian Contributions to Zoology* **511**, 147–149.
- HEANEY, L. R. (1978): Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution* **32**, 29–44.
- LAWLOR, T. E. (1982): The evolution of body size in mammals: evidence from insular populations in Mexico. *Am. Nat.* **119**, 54–72.
- LINDSTEDT, S. L.; BOYCE, M. S. (1985): Seasonality, fasting endurance, and body size in mammals. *Am. Nat.* **125**, 873–878.
- LOMOLINO, M. V. (1985): Body size of mammals on islands: the island rule reexamined. *Am. Nat.* **125**, 873–878.
- MCNAB, B. K. (1976): Seasonal fat reserves of bats in two tropical environments. *Ecol.* **57**, 332–338.
- MORRISON, D. W. (1980): Efficiency of food utilization by fruit bats. *Oecol.* **45** (1), 270–273.
- NORBERG, U. M.; RAYNER, J. M. (1987): Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* **316**, 335–427.
- PACHECO, V.; PATTERSON, B. D. (1992): Systematics and biogeographic analysis of four species of *Sturnira* (Chiroptera: Phyllostomidae), with emphasis on peruvian forms. *Mem. del Mus. de Hist. Nat., U. N. M. S. M. (Lima)* **21**, 57–81.
- PATTERSON, B. (1982): Pleistocene vicariance, montane islands, and the evolutionary divergence of some chipmunks (genus *Eutamias*). *J. Mammalogy* **63**, 387–398.
- RIDGWAY, R. (1912): Color standards and color nomenclature. Washington: Robert Ridgway.
- WENZEL, R. L. (1976): The streblid batflies of Venezuela (Diptera: Streblidae). *Brigham Young Univ. Sci. Bull. Biol. Ser.* **20**, 1–2, 1–177.
- WENZEL, R. L.; TIPTON, V. J.; KUEWKLICZ, A. (1966): The streblid batflies of Panamá (Diptera Calyptera: Streblidae). In: *Ectoparasites of Panamá*. Ed. by R. L. WENZEL and V. J. TIPTON. Chicago: Field Museum Nat.
- WILKINSON, L.; HILL, M.; WELNA, J. P.; BIRKENBEUEL, G. K. (1992) SYSTAT for Windows: Statistics, version 5 ed. Evanston, IL: Systat Inc.
- WILSON, D. E. (1991): Mammals of the Tres Mariás Islands. *Bull. Am. Mus. Nat. Hist.* **206**, 214–250.

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